

CONTRIBUTION FROM THE CRYPTOGAMIC LABORATORY OF HARVARD UNIVERSITY. XLIII.

NOTE ON THE STRUCTURE AND REPRODUCTION OF COMPSOPOGON.¹

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(WITH PLATE XXI)

THE genus *Compsopogon* Mont., which is the sole representative of the Compsopogonaceæ, includes a few described species of filamentous algæ inhabiting the warmer regions of the earth, which are distinguished in general by their characteristic bluish or violet-green color, recalling that of some of the Myxophyceæ; while they are structurally peculiar from the fact that their filaments consist of an axial row of very large cells surrounded by one or more layers of corticating cells, the resultant structure closely resembling that of *Ceramium* among the Florideæ, though originating in a very different fashion.

The reproduction of these plants, although it has been very accurately interpreted by Schmitz (Engler & Prantl, Die nat. Pflanzenf., Algæ, p. 318) from an examination of dead material, has never so far as I am aware been directly observed, and since during a recent botanizing expedition in Florida I had an opportunity to study an abundance of fresh material, a special effort was made to obtain definite information on this point.

This alga was first met with at Cocoanut Grove in November 1897 along the shores of Biscayne Bay, growing most abundantly beside the road to Miami just north of the village, in ditches fed by bubbling springs which doubtless originating in the Everglades and traversing the narrow intervening strip of coral rock formation emerge in all directions along the bay and even mingle with the salt water at some distance from the shore.

¹The substance of this Note was read at the New Haven meeting of the Society for Plant Morphology and Physiology, December 27, 1899.

The water along the margins of the bay is consequently in many places largely diluted in this way, so that, although the ditches above mentioned were repeatedly covered by the high tides during my stay, the water they contained was seldom perceptibly brackish.

A second locality was found at Daytona, a more northern station on the Halifax "river," where the alga occurs abundantly quite above and beyond any tidal influence in the rapidly flowing waters of the "canals," several of which intersect the town toward the south at right angles to the shores of the "river." A large mass was also found floating in a stagnant ditch on the Port Orange road south of Daytona, and it was seen to be conspicuously abundant in a brook which crosses the railroad just north of the New Smyrna station; while lastly a quantity was found on the margin of the St. John's river just below Jacksonville. In this connection it may be mentioned that specimens in the Herbarium at Harvard sent by Mrs. Curtiss are said to have been found in "tidal water" in the Hillsborough river near Tampa in west Florida; while it is further reported from Greencove and Blue Springs in the St. John's river region, as well as from Jupiter inlet on the east coast.

It is thus evident that *Compsopogon* is widely distributed and probably common in Florida; and that, although it may occur in tidal water that is practically fresh, it is characteristically an inhabitant of waters in which there is no admixture of salt.

Concerning the species of *Compsopogon* very little appears to be known and but few forms have been described; the brief list, exclusive of one or two uncertain species, comprising *C. leptoclados* Mont., from Guiana; *C. chalybeus* Kuetz., from Guiana, Porto Rico, and Florida; *C. aeruginosus* (J. Ag.) Kuetz., from Cuba; *C. coeruleus* (Balbis) Mont., from Florida, the Antilles, and Algeria; and *C. Corinaldi* (Menegh.) Kuetz., which has an apparently very limited distribution in Italy; to which, according to De Toni (*Sylloge* 4: 29), should be added *C. lividus* (Hooker) De Toni from Madras. That some of these are merely synonyms seems hardly doubtful, and so far as can be

determined by published figures and descriptions few of them appear to be distinguished by characters that might not be included in the variations of a single species.

In regard to the specific determination of the species which I examined in Florida it should be mentioned that the form occurring at and near Daytona has been kindly compared by M. Bornet with specimens of *C. coeruleus* from Porto Rico in Montagne's herbarium with which it seems to be beyond question identical. The Cocoanut Grove material, however, though it can hardly be separated by any distinctive microscopic characters, is macroscopically strikingly different when fresh, being paler greenish in color, soft and pliable to the touch, and much smaller: for though its filaments are rarely more than five or six inches long those of the Daytona material normally attain a length of two feet or more, their diameter being proportionately greater; while the whole plant has a characteristically harsh stiff feel and a deeper and more striking violet-blue-green color.

Whether these peculiarities should be attributed to a specific difference, or whether they merely represent variations of a single species due to a slight difference of environment resulting from the presence or absence of tidal influence, for example, is uncertain. In either case the younger filaments and their branches consist of single rows of rather flattish cells with numerous oval to oblong or nearly spherical chloroplasts, some of which lie immediately about the conspicuous nucleus; while the greater part are peripherally disposed, being held in a protoplasmic reticulum (*fig. 1*), the active circulation in which is very conspicuous. These chloroplasts, which often exhibit a slow change of position in the protoplasmic mesh, vary but slightly in shape, and in no instance were any elongate or thread-like forms seen like those described and figured by Schmitz (*l. c.*) as characteristic of *C. coeruleus*. The filaments increase in length through intercalary divisions, and at no great distance from the terminal cell longitudinal septa begin to make their appearance, irregularly at first, but succeeding one another in such a fashion that a central axial cell comes to be separated from a layer of peripheral

cells that completely surround it and continue to undergo anticlinal divisions without regularity, while the axial cell constantly enlarges, assuming a flattened barrel-shaped form. The originally single cells of the younger filaments are thus converted into corticated segments indicated by slight constrictions in the older filaments; the monstrosously developed axial cells, which are filled with watery contents and contain few chloroplasts, forming a continuous series (*fig. 14*). The corticating cells which are irregularly polygonal (*fig. 7*) form, according to Schmitz, but a single layer even in the oldest filaments; but although this seems to be invariably the case in the material from Cocoanut Grove, as shown in the figure last cited, it by no means applies to the Daytona form in which, although the original axial cells appear to remain undivided, periclinal divisions take place by which the corticating cells are separated into two well-defined layers (*fig. 12*), as is also indicated in Kuetzing's *Tabulae Phycologicae* 7: *pl. 88, figs. b and f*, which may be increased to three or even four in older axes like that shown in *fig. 13*, a portion of the axial cell being indicated at *x*.

The filaments of *Compsopogon* are always more or less copiously branched, and although short secondary branches are sometimes developed from the corticating cells, the primary ones appear in all cases to be formed by the direct outgrowth of one of the undivided cells of the younger filaments. The alga when growing in still water may remain unattached, but is usually fixed to sticks, stones, or other plants, a short series of cells at the base remaining uncorticated and sending down rhizoidal outgrowths which form an attachment analogous to that of *Porphyra*.

An examination of the Cocoanut Grove material showed further that, although the cells of a majority of the plants gave no indication of any differentiation that might suggest a preparation for some form of reproduction, in others the cells of the cortex as well as those of the younger uncorticated branches had evidently divided in a characteristic fashion; one, usually the smaller of the two resultant cells, being conspicuously differentiated by reason of its darker color and more dense contents;

but although these cells were kept under observation for several hours during the afternoon and evening of the day on which they were collected no separation of spores was noticed. On the following morning, however, the dark cells were found to have disappeared, while the filaments presented the normal appearance. Although no empty cells were visible from which spores might have escaped, it was evident that something of this nature had occurred during the night. A second attempt was therefore made on the following evening; but nothing having transpired, a filament, in which many hundreds of these dark cells were present, was placed in a Van Tieghem cell shortly after nine o'clock and left till morning, when it was found to have resumed its normal appearance as before. In place of the dark cells, however, which had disappeared, a corresponding number of spherical green free cells were found lying motionless in the water at a short and rather constant distance from the filament, having evidently escaped during the night. Observations were therefore resumed at a later hour on the following evening, and at about eleven o'clock I was rewarded by seeing the first aplanospore make its escape. The same type of reproduction was repeatedly observed on subsequent occasions, and may be summarized as follows:

Formation of macroaplanospores.—Any of the superficial corticating cells, even in the oldest portions of the plant, or any of the cells of the younger filaments, even before the divisions preceding cortication have taken place, may become separated during the night into two daughter cells, in one of which the contents is more dense than in the other, and the nucleus larger and more conspicuous. As the day advances the oval chloroplasts by repeated division eventually fill it almost completely, and it begins to assume a sub-triangular outline; one of the rounded angles projecting in the form of a papilla, the wall of which is more or less distinctly thickened, the contents just beneath it becoming nearly or quite free from chloroplasts (*fig. 1*). As this cell or monosporangium matures, the basal septum by which it was originally separated from the other

daughter cell bulges more and more strongly towards the latter, and finally the discharge of the spore is accomplished, as in other instances where a papilla for dehiscence is formed, slowly at first and then more rapidly; while during its discharge, the basal septum reverses its position, the pressure exerted by the contents of the adjacent cell pushing it back into the monosporangium as the latter empties (*figs. 2-4*), the process continuing after the spore has escaped until the cavity is wholly obliterated, so that in a few hours the position of the sporangium is merely indicated by the slightly projecting margins of the orifice through which the spore escaped.

The spore, which is discharged with a force only sufficient to carry it a very short distance from the filament, is quite spherical, completely filled with chloroplasts, except for a small area (*fig. 5*) which is free from them, and possesses not even a slight amoeboid motion. In the Van Tieghem cell a few of the spores became disorganized in a short time, while a great majority, secreting a distinct wall, began to germinate on the day following their discharge; and the young plants thus formed continued to grow, forming branching filaments, for more than a week, when the culture had to be abandoned.

This type of reproduction, which was frequently met with in the material examined at Cocoanut Grove as well as at Daytona, was very uniform in all cases, but just as I was preparing to leave the former locality, a tuft of small plants was found growing on submerged grass culms in water more than usually subject to tidal influence, among which forms having the normal type of sporulation were associated with others in which it was somewhat different. Although the peculiar characteristics of this second type of sporulation may be the result of unfavorable conditions and without special significance, it may be convenient on account of their small size to distinguish the spores formed in connection with it as microaplanospores.

Formation of microaplanospores.—The formation of the cells destined to produce microaplanospores resembles the first steps in the formation of the macroaplanosporangia in that any cells

of the cortex or of the younger uncorticated portions of the filaments may divide to form two cells, one of which is usually, however, far smaller than the other and often separated from it (*fig. 10*) by an oblique septum. These small cells, instead of being converted directly into sporangia, become pushed outward so as to occupy a more or less peripheral position, and soon begin to divide independently, at first by anticlinal septa only, the early divisions sometimes following one another at right angles with such regularity that the resultant cells may be in many cases so conspicuously arranged in groups of four as to suggest aggregations of tetraspores; a resemblance, however, which soon disappears, since the divisions follow one another with increasing irregularity, and may even become periclinal. The filaments thus become covered with scattered sori (*figs. 8, 11*) irregular in form as well as in the number of cells which compose them, and might well be mistaken for groups of parasitic algæ having a habit somewhat resembling that of *Xenococcus*.

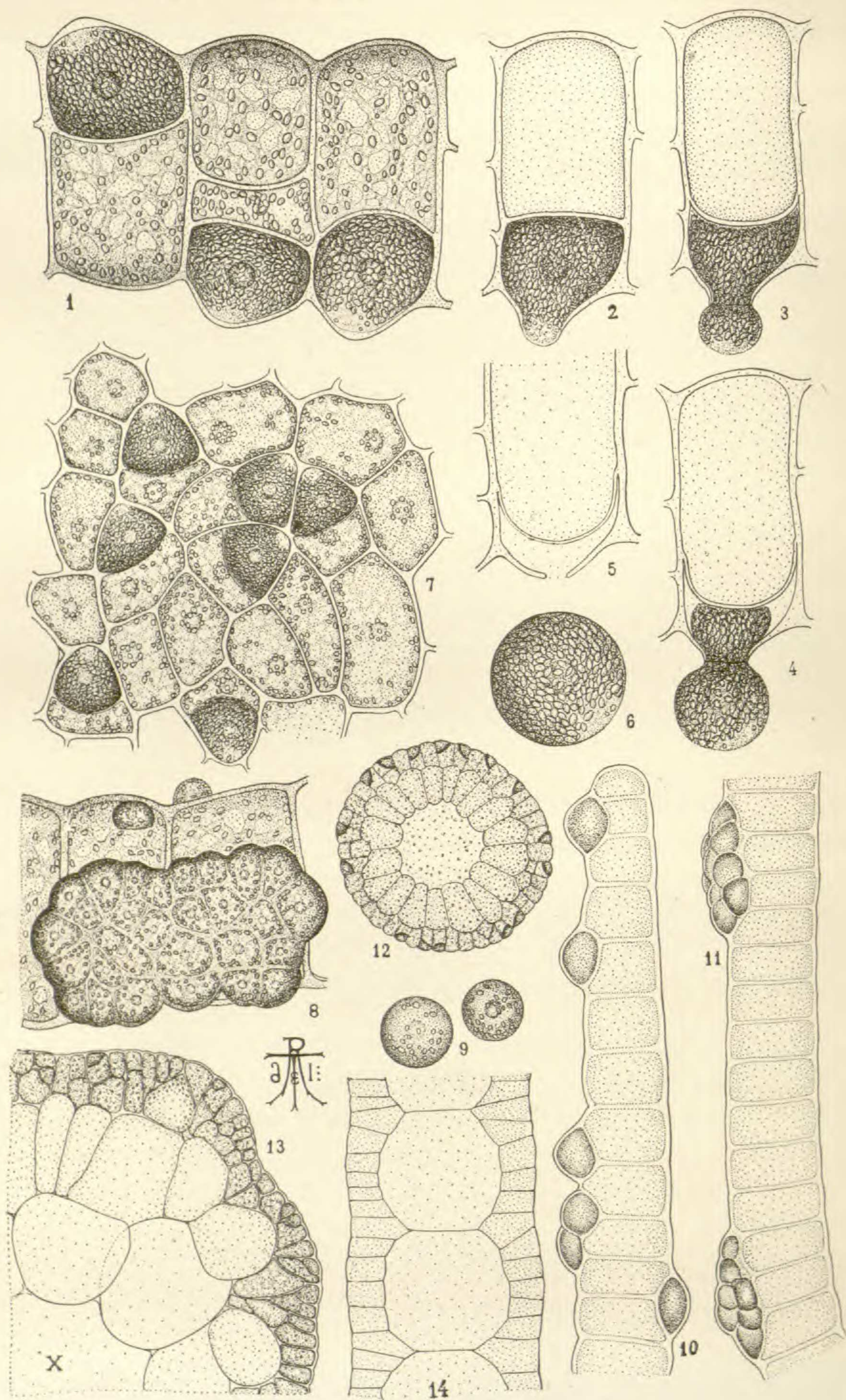
The discharge of spores from the cells composing these sori was not actually observed, but preparations left over night in Van Tieghem cells showed that such a discharge undoubtedly takes place, the sori being surrounded by numerous aplanospores, which, like those of the normal type, were spherical and from their regular position evidently non-motile; but were, on the other hand, far smaller (*fig. 9*) and paler from the presence of a relatively much smaller number of chloroplasts. That these microaplanospores are similar in nature to the normal spores, and that they germinate directly is altogether probable; but the exigencies of my departure made it impossible for me to determine this as well as other points in connection with them. The appearance of the older sori suggests the conditions that have been figured in connection with the supposed formation of antherozoids in *Bangia*; but there was no indication that the bodies thus separated in *Compsopogon* were sexual in function.

A careful examination of the coloring matter of these plants would be a matter of no little interest, and it may be worthy of

mention that it is so readily soluble that the bowl of water used for mounting some of the dark colored Daytona material was soon tinged a deep, somewhat violet-blue, suggesting a slight mixture of phycoerythrin with phycocyanin.

The facts above presented, although they furnish definite information concerning the reproduction of this peculiar group, are not such as to make the true position of its members less obscure than they have been heretofore, since in general they substantiate the conclusions reached by Schmitz, based, as has been previously mentioned, on the examination of dead material. As this author has pointed out, their resemblance to forms like *Ceramium* in the gross structure of the thallus is wholly superficial, the cortications originating very differently in the two cases, and it seems quite certain that their near relatives are not to be sought among the higher Rhodophyceæ. It cannot be denied, however, that, so far as they are known, their reproductive processes are more directly comparable with those of the Bangiaceæ than of any other group, the aplanospores of *Erythrotrichia* being similar to those of *Compsopogon* and similarly produced. That the paler "microaplanospores" of the latter genus may correspond to the "antherozoids" of the Bangiaceæ is not impossible, and although no indication of any sexual process was observed in the material examined, it may occur under other conditions or at other seasons of the year. Admitting, however, that these bodies are probably not sexual in nature, it may be remarked that the same might be said of bodies to which this function has been attributed among the Bangiaceæ; so that in either case it would seem more in accordance with the ascertained facts to leave the family in question among the doubtful Bangiales, in the absence of any other group to which they seem as closely related. Yet, although this is the position actually assigned to them by Schmitz (*l. c.*), he finally remarks, "Am besten dürfte es sein die Compsopogonaceæ als eine etwas isoliert stehende Gruppe vegetativ hoch entwickelter Formen den grünen Algen zuzuzählen."

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